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Regularities in Phenotypic Variation as a Property of the Developmental System: Evidence from the Evolution of Early Amphibians

M.A. Shishkin

Paleontological Institute, Russian Acad. Sci.; Profsoyuznaya 123, Moscow 117997, Russia

Abstract

An evident non-randomness in the variability of living organisms is caused by the integrity of their developmental systems, which undergo the evolutionary transformation as a whole. The commonest manifestation of such orderliness is the occurrence of homologous variations in related forms. The evolution of the dominant group of early amphibians (Temnospondyli) provides numerous examples of this phenomenon.

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Corresponding Author:
M.A. Shishkin
sch-oks@mail.ru

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1. Introduction

The pattern of the variability of a living organism is obviously predetermined by its evolutionary history. In line with this, the assessment of the array of possibilities which a given type of organization can realize depends on one’s understanding of the evolutionary mechanism. In particular, this concerns reasons that could be used to explain orderliness in organismal variability. The latter is expressed primarily by the presence of similar variations in related forms. This regularity serves as the basis for many generalizations, such as the idea of a homologous variability series (Cope, Vavilov), the law of related deviations (Krenke) or the transitive polymorphism concept (Meyen). To assess this phenomenon in a sound way, of crucial importance is the fact that such parallel variations may occur regardless of whether they represent the stable (heritable) features or just induced effects. In the history of evolutionary thinking, this point was long used to ground Lamarckian views

Attempts that were made attribute parallel variability to an action of homologous or related genes naturally exclude from consideration all non-hereditary variations. Another proposed suggestion (known as the nomothetic approach) tends to assign the discussed phenomenon to universal laws of shaping which operate in the physical world. Such an attempt to reduce a given category of biological orderliness to some non-biological causes looks like an appeal to ignorance.

2. Methodology

The only way to find an integral historical explanation of parallel variability is the organism-focused approach implying that the subject of evolution is a holistic living organization. In this case, all the properties of the latter should result from its systemic nature. This approach is based on the concept of the reaction norm as a species-specific array of developmental trajectories realizable with the present constitution of the zygote.

The fundamental implications from this approach were revealed by Goldschmidt (1), who found that ontogeny is controlled by the integral reaction system determining all the range of phenotypic deviations available for such a system. These cannot be divided into the effects of mutations and those of external agents, but form instead a single set of system responses to disruptions to the due coordination of the formative processes. This set is stated to undergo the evolutionary transformation as a whole. This principle in turn underlies the epigenetic theory of evolution (ETE), based on generalizations by Schmalhausen (2) and Waddington (8); cf. Shishkin (5,6).

According to ETE, understanding the nature of individual variations proceeds from the following premises. The balance of organisms with their setting is expressed as a uniformity (equifinality) of their adult norm, which is maintained due to the regulation of development within a wide range of fluctuations of external and internal factors. Outside the conditions allowing such regulation, the norm is replaced by a range of unstable variations indicating the loss of system equilibrium.

Taken as a whole, the space for such potential aberrations of the living system is regarded as its specific property, in the same way as this holds for the normal course of development. It is just that the specific pattern of such alternatives allows the researcher to recognize some orderliness in variability. In a simplified form, the overall set of developmental trajectories realizable for a system can be expressed as the model of the epigenetic landscape by Waddington (8).

Evolutionary change of the developmental system is a transformation of its epigenetic landscape. The driving force behind this shift is the restructuring of the system (by selection) towards the reparation of its stability under new environmental conditions. The sequence of steps in this process is as follows. 1. The triggering event is the loss of stability of the terminal state of system (replacement of the adult norm by its aberrations). 2. The system begins to search for a new equilibrium by selecting carriers of the most viable aberration. Hence, the nearest model of the new adult norm is one of deviations of the previous developmental pattern. 3. The stabilization of this morph as a newly formed noise-resistant norm converts its developmental pathway into a standard trajectory of development. This process, i.e. the stabilization of the formative mechanism of the novelty, spreads with the generations towards earlier ontogenetic stages (cf. “phylembryogeneses-consequences” by Severtsov (4)).

In this light, a comparison of a given developmental system with the results of its closest changes (expressed in terms of the space of potential pathways) allows us to predict the following effects. 1. In closely related taxa, the general design of developmental trajectories (valleys of the landscape) should be essentially similar, with the main differences concerning the frequency of their individual realization. 2. A character state known in a certain taxon as an absolute norm may show different grades of stability in other related forms, with ranging from a variant of the norm to a random variation. 3. In line with effect 1, the developmental systems of close relatives must show similar domains (watersheds of the landscape valleys) of the most unlikely or “forbidden” formative events. All these expectations are well known as real properties of homologous variability in modern organisms.

3. Results

The above rules can be also readily exemplified by the morphology of early amphibians, whose commonest fossil group, Temnospondyli, ranged from the Carboniferous to the Early Cretaceous. One of the most remarkable events in its evolution was the formation of a Mesozoic (“stereospondylous”) structural pattern, which was underlain by the ousting of the group from terrestrial biotopes. Most of the basic features of this change relate to a strengthening of the exoskeletal ossifications (along with increasing reduction of endocranial bones). In particular, notable are the backward extension of the cheek-skull roof suture and the pterygo-parasphenoid suture; the loss of both the pterygo-vomerine contact and occipital exposure of the otic capsule; the appearance of the postglenoid division of the mandible, etc. The Triassic groups that realized these changes in parallel are (at least) the Capitosauromorpha, the advanced Trimerorhachomorpha (including metoposaurs), the Plagiosauria and the Rhytidostea. The current uniform trend to unite these lineages into a monophyletic clade Stereospondyli (3,9) is based on the cladistic presumption that constructing a credible phylogeny should rely on minimizing the number of homoplasies. But this belief can be countered with the evident fact that the formation of major organization novelties (such as the rise of arthropods, mammals or birds) proceeded as extensive homoplastic evolution. Turning to the morphotypes of Mesozoic temnospondyl lineages, it may be reasonably concluded that their basic uniformity indirectly testifies the similarity of variation patterns of their immediate progenitors.

An overall proximity of variation ranges in temnospondyls is equally evidenced by the fact that the individual deviations occurring in many taxa may correspond to the stable characters of their more or less distant relatives, up to remote ancestors. Although some such features may be of pedomorphic origin, this does not necessarily mean that they are directly derivable from the standard early ontogeny of the forms compared; instead, they may result (in parallel) from the reactivation of the latent potencies of the given developmental systems. An example of such a novelty is the appearance of the “interfrontal” bone in the skull roof. Known commonly as a sporadic variation, it is stabilized in the family Eryopidae and seems to be produced by the reactivated capability to form the postrostral complex peculiar to the crossopterygians. A similar example is the occasional retention of a median fissure in the adult parasphenoid body. This rare anomaly, only vaguely inferable from the standard temnospondyl ontogeny, reflects the presence of paired paraotic plates behind the true parasphenoid in fish-grade ancestors (7).

One more parallel between the stable adult character (known in some groups) and its abnormal equivalent (sporadically occurring elsewhere) is exemplified by the position of the frontal bone with respect to the orbital margin. In the temnospondyl archetype, the bone is excluded from the margin; the reverse state normally takes place only at the juvenile stages, when the pre- and postfrontal anlagen are too small to isolate the frontal from the orbit. This provisional condition can be pedomorphically retained in the adult in such groups as the Dissorophoidea and, primarily, the Capitosauroidea. On the other hand, the same feature may occur as an anomaly in those taxa that normally demonstrate an alternative (typical) condition. That the derived state seen in capitosaurids evolved from a corresponding variation is indirectly evidenced by the fact that the early members of the family may show both mentioned alternatives of the frontal position as a distinction of generic level.

Spectacular evidence of the changeable status of a given evolutionary novelty is the loss of the intertemporal bone, which evolved in a number of lineages by the bone’s fusion with either the postfrontal or postorbital. Assessed as whole, the role of the first fusion mode fluctuates from being a norm in the overwhelming majority of advanced temnosponyl lineages to an intraspecific variation within the genus Dvinosaurus.

4. Conclusion

The above parallels in the polymorphism of the discussed fossil group, along with fluctuations in the stability and organizational role of the particular implemented variations, confirm the integrity of the evolution of the developmental system. This is one reason why the spectra of potential developmental alternatives in related forms retain a great deal of resemblance and continuity.

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